THE GREEN JAY TURNS BLUE IN PERU: INTERRELATED ASPECTS OF THE ANNUAL CYCLE IN THE ARID TROPICAL ZONE

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ABSTRACT.—We quantitatively assessed the green to blue dorsal color change uniquely demonstrated by populations of the Green Jay (*Cyanocorax yncas longirostris*) inhabiting seasonally dry deciduous woodland in the mid-Marañon Valley of Peru. Other subspecies in South America occupy humid habitats and are dorsally green all year. After a complete molt which ends in concert with the termination of the rainy season in March, Marañon jays have bright yellow-green backs. During the interval until the next annual molt, the dorsal plumage gradually turns to greenish-blue or blue. Starting in August and September, in the latter part of the dry season, the population breeds in this phenotype. Microscopic study revealed that fresh dorsal feathers contained a yellow pigment or pigments near the surfaces of rachi, barbs, and barbules. Older, blue feathers had many broken barbs and barbules and lacked yellow pigment. However, because the keratinous surfaces of rachi, barbs, and barbules of such feathers appeared unworn, abrasion seemed unrelated to the loss of yellow pigment. Instead, autoxidation and accompanying bleaching from exposure to sunlight are implicated in this striking color change. *Received 20 Aug. 1992, accepted 3 Dec. 1992.*

In South America the Green Jay (*Cyanocorax yncas*) occurs in a narrow, sickle-shaped range extending from the foothills and mountains of northern Venezuela, westward into Colombia, and southward along the Andes to northwestern Bolivia (Ridgely and Tudor 1989). Over most of this distribution the species occupies humid montane forest, forest edge, and secondary woodland. In the arid mid-Marañon Valley of Peru, however, Green Jays live in a strikingly different habitat—seasonally dry deciduous woodlands of the Arid Tropical and Arid Subtropical zones (as defined by Parker et al. 1982). These arid zone populations (*C. y. longirostris* Carriker 1933) exist immediately to the west of humid zone populations

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of *C. y. yncas,* the form present in subtropical forest for hundreds of miles over the greater part of the Andes from southern Colombia and Ecuador, through Peru, to Bolivia. Compared with specimens of *C. y. yncas,* individuals of *C. y. longirostris* had relatively long bills, short wings, short tails, paler yellow under-parts, and more bluish-green upper parts. Even freshly molted specimens of *C. y. longirostris* had "a decided bluish wash" on their upper parts "about intermediate between *X. y. yncas* and *X. y. cyanodorsalis*" (Carriker 1933:30). (The Green Jay was placed in the genus *Xanthoura* at that time.) Thus, a distinctive "bluish-backed Green Jay" evidently had differentiated in the dry habitats of the mid-Marañon Valley. Because the species is absent from arid habitats west of the mid-Marañon region (e.g., in coastal northwestern Peru and in western Ecuador [Chapman 1926]), it is plausible that *C. y. longirostris* was derived directly from typical "green-backed Green Jays" (*C. y. yncas*).

Because Carriker studied only eight specimens of *C. y. longirostris,* he was unable to appraise properly the extent of either individual or seasonal variation in color. Furthermore, when Chapman (1917:637) discussed the form *C. y. galeatus* of Colombia and stated that "The amount of blue on the hindhead, nape, and back is apparently largely dependent on age . . . ," the possibility surfaced that the bluish back of *C. y. longirostris* was nothing more than a juvenal feature. Consequently, both the interpretation of bluish-backed individuals and the taxonomic status of Marañon populations of the Green Jay have remained problematical since the original description of *C. y. longirostris.* Accordingly, on four trips taken between 1967 and 1974 to the Departments of Amazonas and Cajamarca, northern Peru, we and our associates collected additional specimens of this poorly known, endemic form. The collection was made during three distinct periods of the year and contains birds representing different age categories and varying stages of plumage wear and molt. Information from these specimens outlines the manner in which annual cycles of color change, molt, and breeding are integrated in the Green Jays of an arid, seasonal environment which is unique for the species in South America.

METHODS

The new series of 52 specimens was divided into three samples for analysis: Mar. 2–5 (17 specimens), Aug. 20–Sept. 9 (25), and Nov. 4–23 (10). For quantitative study of coloration of the center of the dorsum, a subset of 42 specimens was examined with a Bausch and Lomb 505 Recording Spectrophotometer equipped with a visible reflectance attachment. Ten specimens with ruffled dorsal feather surfaces were excluded. Flatness of the 100% line was maintained within limits of 1.0% peak-to-peak and flatness of the 0% line, within 0.5%. From trichromatic coefficients (*x, y, z*), obtained from curves of percentage diffuse spectral reflectance between 400 and 700 nm by the 10 selected ordinate method of Hardy (1936:

49–51), dominant wavelength (λ_d), brightness (Y), and excitation purity (P_e) were computed according to table 6 of Judd (1933:371), using the ratios described in Johnson and Brush (1972:247). To expose ensheathed feathers which provided evidence for molt, layers of plumage on each specimen were gently lifted with a dissecting needle under a fluorescent magnifying lamp. For study of the effects of wear on pigment concentration in the shafts, barbs, and barbules, individual fresh and abraded feathers were flattened on slides, flooded with Permount, and examined under 40× magnification with a dissecting microscope and under both 100× and 1000× magnification with a compound microscope. Testis volume was approximated by converting specimen tag figures on testis length and width with the formula for the volume of a cylinder: testis volume = testis width^2 × 0.7854 × testis length. Thus, a specimen with tag data "testis 6 × 4 mm" was estimated to have a testis volume of 75.4 mm^3 (4^2 × 0.7854 × 6).

Age determination. —Green Jays in juvenal (first prebasic) plumage have pale yellowish-white ventral feathers with a distinctive fluffy or loose texture that contrasts greatly with the vivid lemon yellow, solid texture of ventral feathers of subsequent generations. Age of individuals up to approximately the middle of the first postnuptial molt (adult prebasic molt) is easily determined because the postjuvenal molt (first prebasic molt) is partial and results in the retention of narrow rectrices with distinctively pointed or rounded tips that contrast with the broader rectrices with the blunt or truncate tips of adults. (Emlen [1936] and Pitelka [1945] pioneered the use of these ageing criteria in corvids with examples from *Corvus* and *Aphelocoma,* respectively. Pyle et al. [1987:67] extended this methodology to North and Middle American populations of the Green Jay. Because those populations may comprise a species different from the South American populations dealt with here [Hilty and Brown 1986, Ridgely and Tudor 1989], the detailed applicability of their descriptions of molts and ageing criteria to *C. y. longirostris* is uncertain.)

RESULTS

Molt cycles. —Twenty-three specimens were in various stages of molt. Six skins showed postjuvenal molt of body plumage: of three taken March 4–9, two were in heavy molt and one was categorized as in medium-late molt; and three specimens taken August 26–30 were in early to middle stages of the postjuvenal molt. None of the six specimens in postjuvenal molt was replacing flight feathers. The remaining 14 specimens in the March sample were all in middle to late postnuptial molt (second prebasic molt) which is complete in this species. One of the March skins and a specimen taken November 23 are of birds undergoing their first complete postnuptial molt; they are preparing to replace worn, pointy juvenal rectrices and have adult skull pneumatization. Two of 25 individuals in the August–September sample are in what we interpret to be a prenuptial (prealternate) molt in which body feathers but no remiges are replaced. One of these birds has ensheathed central rectrices. It is clear that the postnuptial molt occurs well into March and appears to involve the entire population. In contrast, 20 of 25 August–September specimens were not molting. Three of the molting individuals were young birds in the post-juvenal molt and the remaining two were adults showing limited prenuptial molt. The November sample is also comprised largely of non-molting

birds (9 of 10). The single molting individual was in early first postnuptial molt.

Seasonal color change.—Birds completing the postnuptial molt in March had bright yellow-green or yellowish-green backs, with old and worn blue feathers scattered throughout, and bright green on the upper surface of the rectrices. The August–September sample was extremely variable; color of the back and dorsal surface of the tail ranged from yellow-green or yellowish-green all the way to blue-green. In striking contrast, by November all but two birds were dorsally bluish-green or greenish-blue. This color change is shown clearly on a chromaticity diagram (Fig. 1) in which the dominant wavelength or hue of any single specimen is identified by a straight line which starts at the white point (coordinates for white light of equal energy) and passes through the coordinates of any single specimen on a direct course toward the periphery of the diagram (see legend to Fig. 1 and Rossotti 1983:154–166 for further explanation).

Microscopic comparisons of fresh versus old back feathers revealed that the yellow pigment or pigments responsible for the green color of fresh feathers occurred only near the surfaces of feather rachi, barbs, and basally on the barbules; medially and distally the barbules appeared to be either unpigmented or pigmented only with melanin. The superficial yellow pigment(s) found in the new, green feathers presumably is a carotenoid. Old back feathers appeared blue upon overall visual inspection. Under 40× magnification, however, blue was reflected only by the barbs; the shafts and barbules appeared dusky, perhaps as a result of melanin deposition. At higher power, neither yellow nor blue was reflected and the areas of blue feathers which had been occupied by yellow pigment in green feathers were translucent white, indicating the loss of the yellow pigment in the blue feathers. Although many barbs of old blue feathers had broken tips, and the barbules were in greater disarray than in fresh feathers, microscopic examination under magnification from 40× to 1000× of the surfaces of the rachi, all barbs including those which had broken tips, and barbules of old blue dorsal feathers revealed them to be intact. The physical appearance of surfaces of fresh feathers and old feathers was identical microscopically.

Spectrophotometric analysis enabled quantification and statistical testing of differences in dominant wavelength, brightness, and purity for the three seasonal samples. Between March and November, mean dominant wavelength changed from 564.9 nm (yellow-green) to 495.0 nm (bluish-green) (Fig. 2a); mean brightness decreased from 10.7% to 9.0% (Fig. 2b); and mean purity was reduced from 30.5% to 7.9% (Fig. 2c). For each character a Kruskal-Wallis Test (Sokal and Rohlf 1969:388–391) demonstrated significant seasonal differences (Adjusted H = 23.48 for dom-
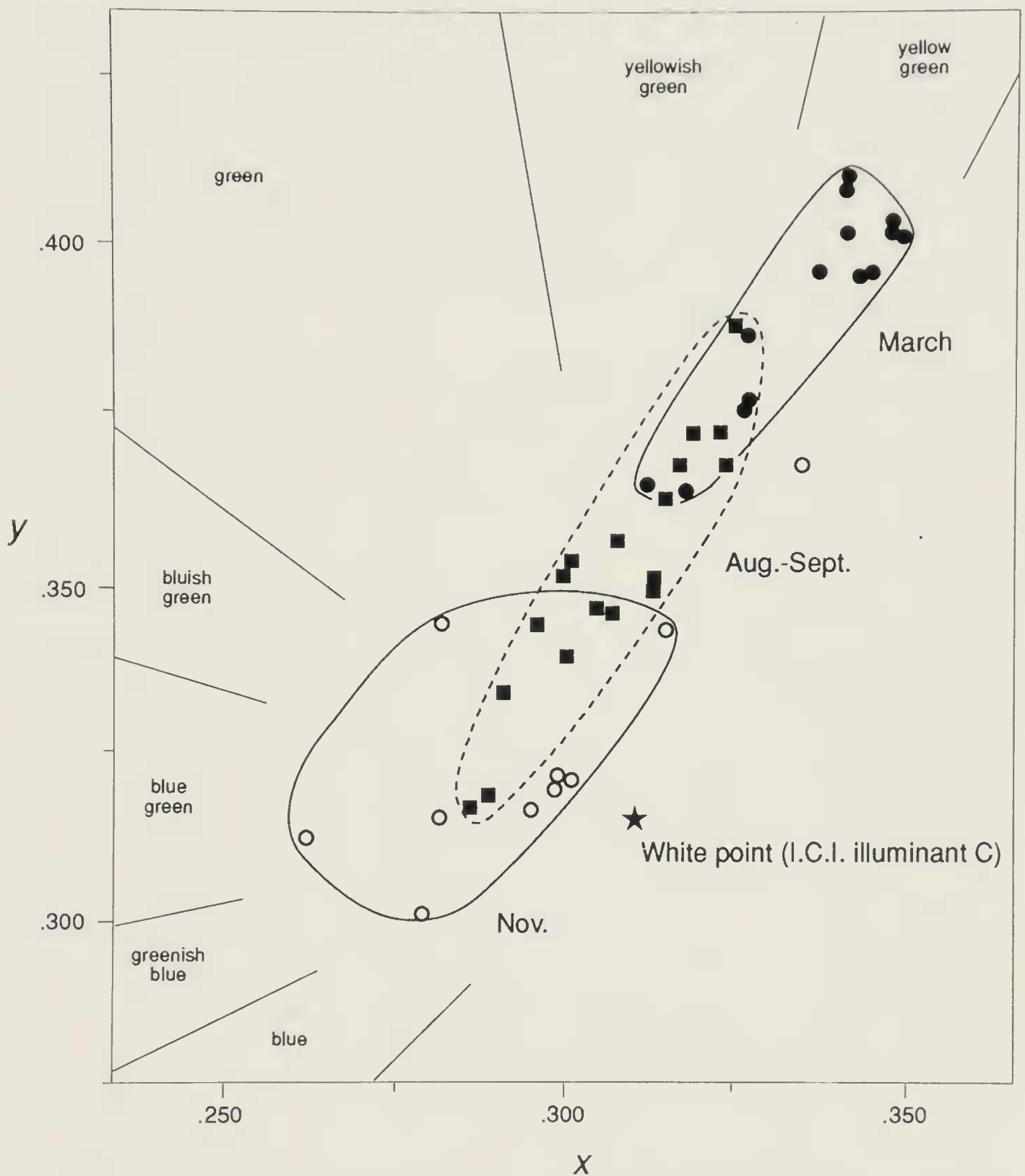
FIG. 1. Chromaticity diagram on which are plotted the coordinates of trichromatic coefficients x and y which resulted from reflectance spectrophotometry of the central dorsum of 42 specimens of *C. y. longirostris*. The total sample was subdivided into three seasonal samples. Coordinates for the white point of I. C. I. Illuminant C: $x_w = 0.3101$, $y_w = 0.3163$. One specimen, a first-year bird with a greenish back, had atypical coordinates for November and was excluded from the main ellipse for that subsample. Approximate ranges of dominant wavelengths for the color names shown are: blue, 465–482 nm; greenish-blue, 482–487 nm; blue-green, 487–493 nm; bluish-green, 493–497 nm; green, 497–530 nm; yellowish-green, 530–559 nm; and yellow-green, 559–571 nm.
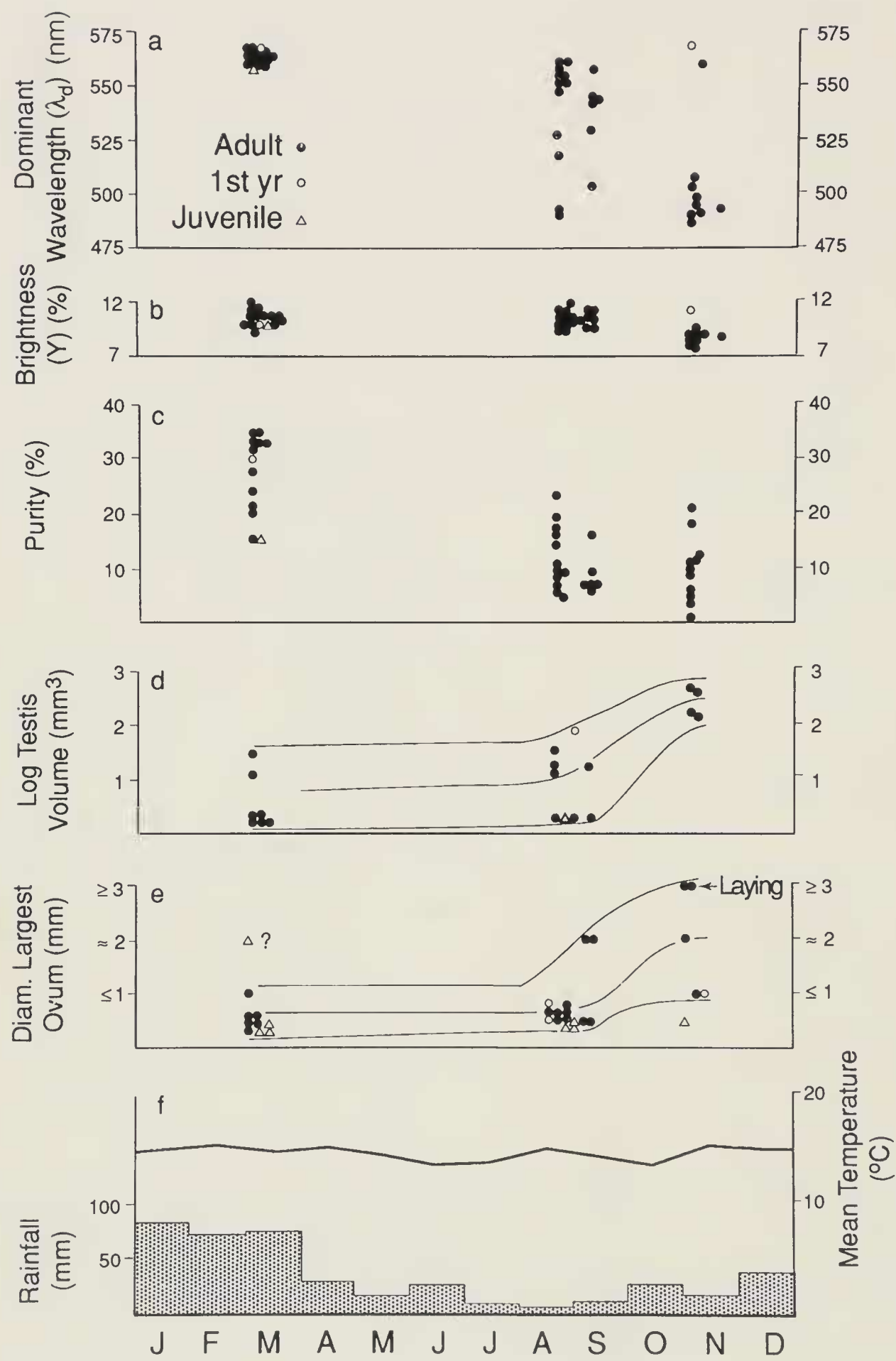
FIG. 2. Interrelated aspects of the annual cycle of the Green Jay in the mid-Marañon drainage, northern Peru: (a–c), components of dorsal color determined by reflectance spectrophotometry, (d, e), reproductive stage of individual specimens; (f), unpublished figures (provided by Manuel Plenge) for monthly mean rainfall and mean temperature for 1951–1960 at Huancabamba, northern Peru, a site near the range of *C. y. longirostris*.

inant wavelength, 15.08 for brightness, and 23.38 for purity and $\chi^2_{.01[2]}$ = 9.210 in each instance, thus rejecting the null hypothesis. Seven of nine pairwise comparisons showed significant or highly significant differences (Mann-Whitney *U*-Test). The two non-significant comparisons were of brightness, March vs Aug.–Sept. (*t* statistic, 135; *z* value, 0.3419; *P* = 0.7324), and purity, Aug.–Sept. vs Nov. (*t* statistic, 105.5; *z* value, 0.743168; *P* = 0.4574). To our knowledge no quantitative study of seasonal color change with such dramatic visual effects has been published previously.

Reproductive cycles.—Male Green Jays in the Marañon drainage undergo definite testicular recrudescence in August and September, and by November the largest testes were recorded (Fig. 2d). The female reproductive cycle (Fig. 2e) parallels that of the male, with enlarging ova recorded in early September and laying individuals found in early November. The data are too spotty to rule out breeding by at least occasional individuals at other times of the year. Indeed, the presence of three late August specimens in early-middle postjuvenal molt suggests that some birds nest from May to July. However, our data definitely indicate that the peak in breeding effort occurs sometime during the Austral spring and summer, i.e., between August and January. We infer that the principal breeding period wanes at least by January or February; by then most birds must be well into the postnuptial molt as shown by the advanced molt stages of the early March sample.

Climatic variables.—The possible relationship of environmental variables such as temperature and rainfall to breeding and molting cycles is of interest. Although mean temperatures are slightly reduced for at least some months during the period April–September (Fig. 2f), the data available point to no pronounced annual variation in this feature. Rainfall totals, however, show clear monthly variability, with a very dry interval between July and September contrasting with a wet season that peaks from January through March (Fig. 2f). Rainfall data from Jaen (Espejo 1971), within the range of *C. y. longirostris*, are very similar except that mean September totals are much greater; for this site September is best included in the wet season.

DISCUSSION

We document that Green Jays in fresh plumage, acquired via a complete molt which ends on a population basis sometime in March, have bright yellow-green backs and that this appearance coincides with the end of the rainy season. From that time on, the dorsal plumage gradually turns to greenish-blue or blue as it increases in age, from the end of the wet season through the ensuing dry season. During the latter part of the dry season

the birds begin to breed while in their bluish phenotype. The extreme in annual blueness is reached just before the major annual molt, which is inferred to begin sometime in January or February, at the height of the rainy season.

At least some instances of color change from green to blue in birds are said to be mediated by degradation through wear of the yellow carotenoid layer in the keratinous sheaths of the feather barbs and barbules. Such wear gradually exposes the Tyndall blue caused by the underlying ho-mogeneous cloudy layer (Lucas and Stettenheim 1972, Fox 1976). Our microscopic study of old blue feathers revealed no apparent wear of the keratinous sheaths of either the rachi, barbs, or barbules, and from this evidence we conclude that abrasion probably does not play a significant role in loss of the yellow pigment. Nonetheless, more refined examination of surfaces of rachi, barbs, and barbules, perhaps through scanning elec-tron microscopy, might detect subtle differences in wear between fresh and old feathers, and we encourage such study.

In a general review of the chemical characteristics of carotenoids, Fox (1976:68) reported that these pigments show "more or less pronounced instability toward atmospheric oxygen (autoxidation accompanied by bleaching of color)." Lucas and Stettenheim (1972:418) directly impli-cated exposure to sunlight in the fading of carotenoid pigments found in bird plumage. A specific example was cited by Welty and Baptista (1988) who state that in the tropical Green Magpie (*Cissa chinensis*) the "plumage is green in forest populations but blue among birds living in open country where sunlight fades the superficial yellow pigment." Unfortunately, no data supporting the conclusion of fading were offered by Welty and Bap-tista, nor have we been able to find a reference that documents their report. Nonetheless, Völker (1964) reported that carotenoids and por-phyrins ("fugitive pigments") faded as a result of exposure to light, and Test (1940) offered direct experimental evidence for the fading of carot-enoids in *Colaptes*. Whether exposure to atmospheric oxygen exacerbates the effects of sunlight, or plays a role of its own in the fading of feathers, continues to be unclear.

For the present example of color change from green to blue in *C. y. longirostris,* the lack of physical evidence for wear on the keratinous surfaces of old feathers leaves us to suspect that autoxidation with ac-companying bleaching (fading) is the most probable cause. Experimental evidence on this point should be sought. The role of sunlight as a catalyst in the oxidation of carotenoids (Test 1940) is likely because individual jays with the bluest backs are found at the end of the dry season when accumulated exposure to sunlight presumably has been greatest.

Is the change from green to blue somehow adaptive? Burtt's (1986) elegant study underscores the complexity of interacting selection pressures that impinge on avian colors and patterns. Regarding dorsal coloration, Burtt noted the probable importance of selection for crypsis because "green, brown, and gray are the least conspicuous feather colors when viewed against a broadleaf or coniferous canopy." We speculate that dorsal color and its seasonal change from green to blue in *C. y. longirostris* is adaptive. Newly molted, dorsally green birds predominate at the end of the rainy season when green background vegetation is most luxuriant. The bluish dorsum could be similarly protective during the dry season, when browns and grays are commoner in the environment. A beneficial effect of crypsis would not necessarily rule out other adaptive physiological or optical relationships between the phenotype of the Green Jay and the biotic and abiotic environment it occupies.

With a South American distribution spanning approximately 28° of latitude (from 11°N Lat. to 17°S Lat.) across the equator, variation in timing of nesting among populations of the Green Jay is of unusual interest. To our knowledge no information on the timing of breeding in mid-Marañon Valley populations at approximately 6°S Latitude has previously been published. Documentation presented here for their nesting in the Austral spring and summer (September to December or January) contrasts strikingly with the "northern" peak breeding period of March and April reported for Colombian populations at approximately 6°N Latitude in "lower montane humid forest" (Alvarez 1975). Therefore, over a latitudinal span of only 12 degrees the species switches the nesting season to opposite periods of the year. Because a pronounced dry season occurred at Alvarez' study site from December through March, coinciding with the *wet* season in the mid-Marañon drainage on the opposite side of the equator, breeding periodicity may be related to rainfall cycles rather than to the relatively weak annual differences in photoperiod in both places. In any event, information on breeding and molting cycles (and associated plumage color change, if any) of populations of the Green Jay occurring between mid-Marañon and Colombian sites would be extremely welcome.

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